

REPORT

Coral reef cascades and the indirect effects of predator removal by exploitation

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Abstract

Fisheries exploitation provides the opportunity to examine the ecosystem-scale biodiversity consequences of predator removal. We document predatory reef fish densities, coral-eating starfish densities and coral reef structure along a 13-island gradient of subsistence exploitation in Fiji. Along the fishing intensity gradient, predator densities declined by 61% and starfish densities increased by three orders of magnitude. Reef-building corals and coralline algae declined by 35% and were replaced by non-reef building taxa (mainly filamentous algae), as a result of starfish predation. Starfish populations exhibited thresholds and Allee-type dynamics: population growth was negative under light fishing intensities and high predator densities, and positive on islands with higher fishing intensities and low predator densities. These results suggest the depletion of functionally important consumer species by exploitation can indirectly influence coral reef ecosystem structure and function at the scale of islands.

Keywords

Allee effect, biodiversity, ecosystem function, outbreaks, resilience, stability, sustainability.

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INTRODUCTION

Human exploitation of the seas has resulted in a greater than 90% decline in predator abundance worldwide (Jackson *et al.* 2001; Myers & Worm 2003). The collapse in predatory fishes is reflected by the local and regional extinction of more than 50 fish populations in the last century (Bellwood *et al.* 2003; Dulvy *et al.* 2003; Baum & Myers 2004). This rapid loss of a large functional component of shallow water marine biodiversity would be expected to have wider ecosystem consequences. The removal of consumers may have diverse and surprising outcomes (Menge 1997; Webster & Almany 2002) and the effects may be sufficient to influence aspects of marine ecosystem structure and function (Paine 1966; Dayton 1985; Estes & Duggins 1995; Shears & Babcock 2002; Duffy 2003; Steneck *et al.* 2003). Consequently, there is concern that the depletion of consumer fishes by exploitation may indirectly modify the structure and function of marine ecosystems, particularly of diverse systems such as coral reefs (Roberts 1995; Hughes *et al.* 2002; McClanahan *et al.* 2002).

The consequences of removing herbivores from ecosystems are relatively well understood compared with our understanding of the effects of removing predators (Hughes

et al. 2003; Hawkins & Roberts 2004). Exploitation is thought to influence ecosystems via trophic cascades where predator removal results in elevated prey abundance, which in turn influences the base of the food web (Kitchell & Carpenter 1993; Pace *et al.* 1999; Pinnegar *et al.* 2000; Shurin *et al.* 2002). Cascades are more prevalent in less diverse systems such as rocky reefs and lakes, but there is some evidence for urchin and starfish-mediated cascades on coral reefs (Pace *et al.* 1999; McClanahan *et al.* 2002). In addition to cascading effects there is concern that anthropogenic impacts, such as exploitation or eutrophication, have the potential to cause unexpected shifts among multiple stable ecosystem states (May 1977; Scheffer *et al.* 2001; McClanahan *et al.* 2002).

Here, we examine a putative trophic cascade involving predatory fishes, the coral-eating crown-of-thorns starfish (*Acanthaster planci*) and reef-building corals (Ormond *et al.* 1990). The crown-of-thorns starfish feeds upon live corals causing the largest known pest-related disturbances on Indo-Pacific coral reefs and it is regarded as a major management problem (Birkeland & Lucas 1990; McClanahan *et al.* 2002). A number of mechanisms, including hydrography, hurricane disturbance, nutrient inputs and predator removal, have been suggested as

potential causes or modulators of starfish outbreaks (Birkeland & Lucas 1990; Bradbury & Antonelli 1990; Ormond *et al.* 1990). Furthermore, predators can maintain prey in a state of negative population growth at small prey population sizes – an Allee effect (May 1977; Knowlton 1992). A search for dome-shaped patterns of prey population growth with negative growth at small population sizes would provide a test for an Allee effect.

Understanding the ecosystem effects of exploitation may be hindered by time lags (decades to centuries) between the onset of overfishing and the consequent changes in ecological communities, the confounding effects of destructive fishing techniques and other anthropogenic influences (Hughes 1994; Jackson *et al.* 2001). We study a series of 13 relatively pristine Fijian islands to construct a spatial gradient of fishing intensity over which we explore the structure of predatory fish and coral reef communities and starfish dynamics. Here, we show how exploitation-mediated predator removal is linked to starfish outbreaks via an Allee effect, which in turn modulates coral reef ecosystem structure and function.

METHODS

The Fijian study system consists of a series of 13 oceanic islands varying in area of coral reef and human population size (Table 1). An index of fishing intensity was calculated for each island by dividing the human population (1996 census) by the length of reef front (Jennings & Polunin 1997; Dulvy *et al.* 2002). This fishing intensity index has been found to be related to fishing behaviour and activity and correlates well with catch rates and estimates of reef fish yields (Jennings & Polunin 1995, 1996). Fijian fishing

gradients have provided considerable insight into the direct and indirect ecological effects of non-habitat destructive fishing practices on coral reef systems (Jennings & Polunin 1996; Dulvy *et al.* 2002, 2004). The underlying assumption of spatial fishing gradients is that processes structuring the ecological communities of individual islands, e.g. large-scale hydrography or recruitment, are approximately equal across the archipelago and the only differences among islands are variations in human densities and the extent of coral reef (Jennings & Polunin 1997). The validity of this approach depends upon the integrity of replicates, i.e. no movement or interchange of fishers among islands and no poaching by external fishers. Fisher interchange and poaching were negligible owing to the well-defended sea ownership system, the large inter-island distances and paucity of ocean-going craft in the island group. Subsistence fishing for food only was practised using non-destructive fishing gears, mainly spears and hook and line (Dulvy *et al.* 2004). Agriculture is non-intensive, minimizing the degree of terrestrial sediment and nutrient inputs and there is no industrial development or other sources of pollution within 150 km radius of the Lau islands, Fiji.

Predatory fishes, starfish and barrier reef communities were surveyed at 13 islands each varying in fishing intensity (Fig. 1). Ecological censusing was conducted on shallow (7 m chart datum) leeward (western) outer reefs at a total of 13 islands, six of which were surveyed three times over a year (Table 1). Fish and starfish densities were estimated using SCUBA underwater visual census (UVC) in replicate 7 m radius point counts (Jennings & Polunin 1997; Samoilys & Carlos 2000). Six replicate point counts were haphazardly distributed within each area. For the purposes of this study we restricted the definition of predators to include all non-

Table 1 Survey locations and dates, number of areas surveyed, human population size, length of reef front, reef area and fishing intensity index (data sources in Appendix S1)

Island code	Fishing ground (Island)	Cruise 1, April 1999	Cruise 2, November 1999	Cruise 3, February 2000	Number of areas surveyed	Human population	Reef front length (km)	Reef area (km ²)	Fishing intensity (human population km ⁻¹ reef front)
A	Marabo		✓		3	10	7.6	3.5	1.3
B	Tavunasici	✓	✓	✓	3	20	7.6	4.0	2.6
C	Oneata			✓	3	156	48.6	95.0	3.2
D	Namuka-i-lau		✓		3	134	23.5	50.0	5.7
E	Vanuavatu			✓	5	89	14.8	12.5	6.0
F	Vuaqava	✓	✓	✓	3	100	15.1	17.0	6.6
G	Komo		✓		3	150	21.4	34.0	7.0
H	Tuvuca			✓	5	181	17.0	21.0	10.7
I	Totoya	✓	✓	✓	5	806	44.7	19.3	18.0
J	Matuku	✓	✓	✓	6	854	35.0	20.1	24.4
K	Moala	✓	✓	✓	8	1596	60.9	n/a	26.2
L	Kabara	✓	✓	✓	5	1012	23.4	44.5	43.3
M	Lakeba			✓	6	1982	39.8	155.0	49.8

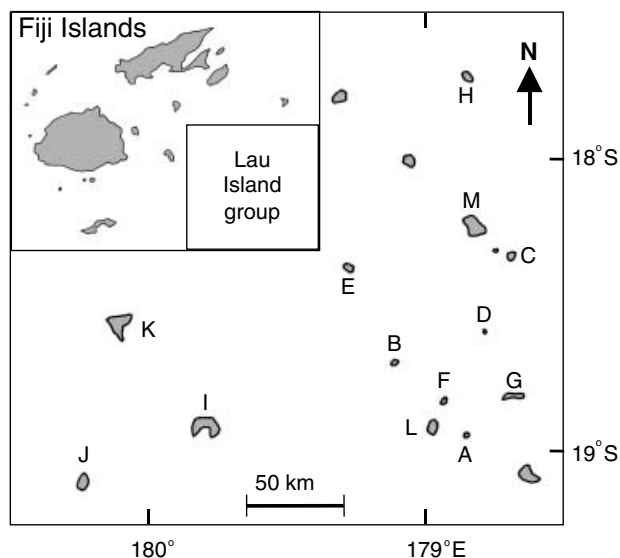


Figure 1 Map of the fishing grounds (islands) studied. Fishing grounds are labelled in ascending alphabetical order of fishing intensity (see Table 1). Inset shows the location of the Lau islands within Fiji.

pelagic reef-associated piscivorous and invertivorous fishes, which totalled 111 species (Table S1). Individuals >8 cm fork length were censused, length was estimated visually and converted to biomass estimates using published length : weight relationships (Dulvy *et al.* 2002, 2004). The surveyor (NKD) was trained in fish size estimation using objects of fixed sizes presented at 3 and 7 m distance underwater and fish size estimation was accurate to within 1 cm (Dulvy *et al.* 2004). Mobile species were censused first followed by sedentary and cryptic species. Individual fish entering the point count during the survey were not recorded (Samoilys & Carlos 2000). Following the fish count, starfish numbers were visually estimated within the area of the point count. The boundary of each point count was first visually estimated, and the radius was confirmed using a tape measure on completion of each count. Underwater visual radius estimates were accurate to within 5 cm. Underwater visibility was >20 m throughout the study and all surveys were conducted in daylight at least 1 h after sunrise and 1 h before sunset. Count time was not standardized because this was dependent on fish abundance, diversity and habitat complexity (Jennings & Polunin 1997). Fish density may be influenced by reef architectural complexity. Rugosity was measured by fitting a 3 m length of small-link chain to the reef surface perpendicular to the reef crest at the centre of each replicate point count. The corresponding horizontal distance was measured by tape and the ratio of chain length : horizontal length calculated. There was no significant variation in chain measures of reef rugosity along the fishing intensity gradient (Dulvy *et al.* 2002).

Percentage cover of each benthic category was calculated by overlaying transparent acetate sheets containing 20 randomly located 1 cm diameter circles over $30 \times 500 \text{ cm}^2$ digital photographs recorded randomly in each of the UVC point counts (Dulvy *et al.* 2002). Reef building benthos included hard corals and coralline algae and non-reef building benthos included ascidians, blue-green algae, filamentous turf algae, fleshy macroalgae, *Palythoa* spp. soft corals and sponges. A stratified sampling design was used to appropriately summarize the small-scale heterogeneity into a large scale perspective, and three to eight areas were surveyed at each island and data were aggregated across survey periods then hierarchically, across replicates, areas and islands (Dulvy *et al.* 2002).

We used a general linear modelling framework to test for the existence of an Allee effect in starfish dynamics. Rates of starfish population change dn/dt could be calculated using two points in time for each of three islands, i.e. $n = 3$, and at three points in time for each of two other islands, i.e. $n = 4$, resulting in a total of $n = 7$. Rates were scaled to per capita rates ($1/n$). A general linear model was then constructed using per capita rate of starfish population change, i.e. $n(t)^{-1} [n(t+1) - n(t)]$ as the response variable, and both $n(t)$ and $n(t)^2$ as predictors. The null expectation is of a negative linear relationship with a positive intercept, consistent with classical Lotka–Volterra dynamics where per capita population growth rate declines as intraspecific competition increases with density, whereas a statistically significant positive quadratic term indicates the dome-shaped relationship of an Allee effect.

RESULTS

The densities of predatory fishes were 61% lower at the most heavily fished islands compared with the most lightly fished islands ($r^2 = 0.59$, $F_{1,11} = 16.3$, $P < 0.001$; Fig. 2a). Starfish were absent at seven islands and present in six islands. At the islands where starfish were present their densities were positively related to fishing intensity ($r^2 = 0.71$, $F_{1,4} = 13.1$, $P < 0.05$; Fig. 2b). The consumption of coral by starfish resulted in mass coral mortality at the island scale. We observed an almost complete evolution of a starfish outbreak over the course of a year at only one of the islands. Starfish densities increased from 8000 to 113 000 individuals km^{-2} and declined to 50 000 individuals km^{-2} over the course of a year at Kabara Island (Fig. 3a). At this island hard coral cover declined from 44 to 8% and the cover of microfilamentous turf algae increased from 22 to 60% (Fig. 3b). The structure of the coral reef communities varied with predator density, the cover of carbonate-accreting reef building benthos was positively correlated with predator density (Fig. 4, $\rho = 0.56$, $t_{11} = 2.314$, $P < 0.05$). Overall, the reefs of lightly fished islands with high predator densities

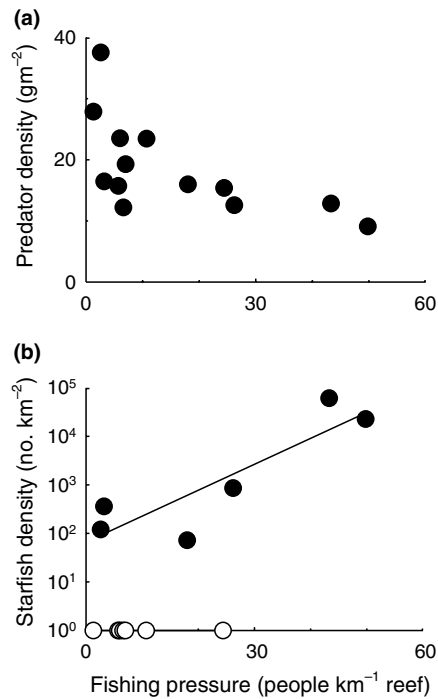


Figure 2 The relationship between fishing intensity and (a) average density of predatory fishes. (b) The relationship between fishing intensity and average density of crown-of-thorns starfish islands where starfish were present (●). Islands without starfish are denoted as (○).

were dominated by carbonate-accreting reef building organisms – scleractinian hard corals and coralline algae (60–75% cover, Fig. 4). In contrast the reefs of the starfish-infested, heavily fished islands with low predator densities were dominated by rapid-colonizing fast-growing non-reef-building species, mainly turf algae (41–60% cover, Fig. 4).

Although the number of observations is small, there is a statistically significant domed relationship between starfish density and per capita population growth rate (significant quadratic term: $F_{1,4} = 8.22$, $P < 0.025$). The outbreak threshold was ≈ 250 (± 235 estimated 95% confidence interval) starfish km^{-2} barrier reef (Appendix S1 in Supplementary Material). Starfish populations below this density exhibited declining population growth and above the threshold starfish populations exhibited positive population growth (Fig. 5a). Small declining starfish populations occurred at islands with lightest fishing intensities (Fig. 5b) and highest densities of predatory fishes (Fig. 5c). Large increasing starfish populations occurred at islands with higher fishing intensities (Fig. 5b) and lowest predator densities (Fig. 5c).

DISCUSSION

Changes in ecosystem state and Allee effects have been suspected in the sea but they have proven exceedingly

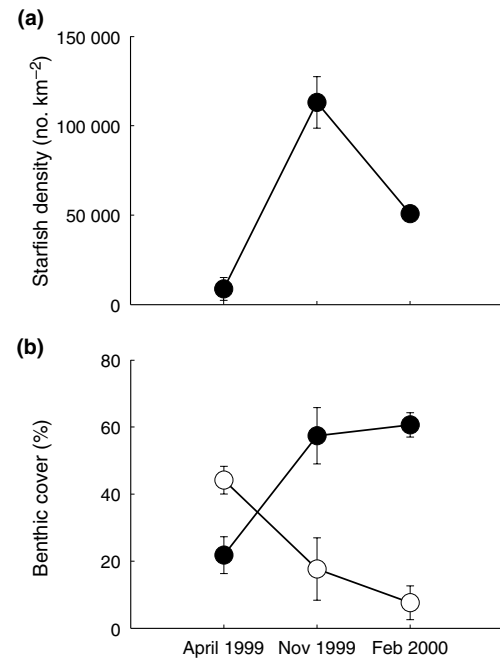


Figure 3 The change in (a) starfish density and (b) percentage cover of hard coral (○) and microfilamentous algae (●) at three time intervals at Kabara Island, which has the second highest fishing intensity, 43.3 people km^{-1} reef front (mean values \pm 95% confidence intervals).

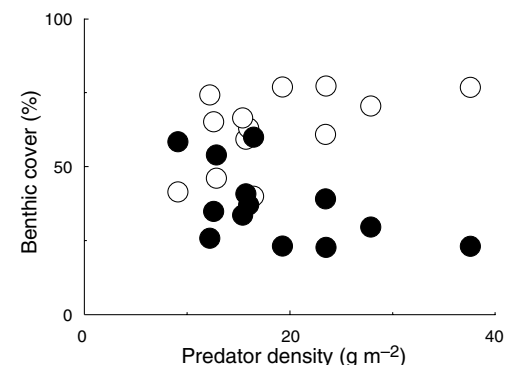


Figure 4 The relationship between predatory fish biomass and per cent cover of reef building (○) and non-reef building (●) benthos. Note the 95% confidence intervals averaged 5% and were less than the point diameter.

difficult to detect at large spatial scales in marine systems (Hughes 1994; Estes & Duggins 1995; McClanahan 1995; Liermann & Hilborn 2001; Scheffer & Carpenter 2003; Steneck *et al.* 2003). Our data suggest that predator removal by subsistence exploitation may be sufficient to allow outbreaks of the crown-of-thorns starfish indirectly resulting in cascading changes in ecosystem structure and

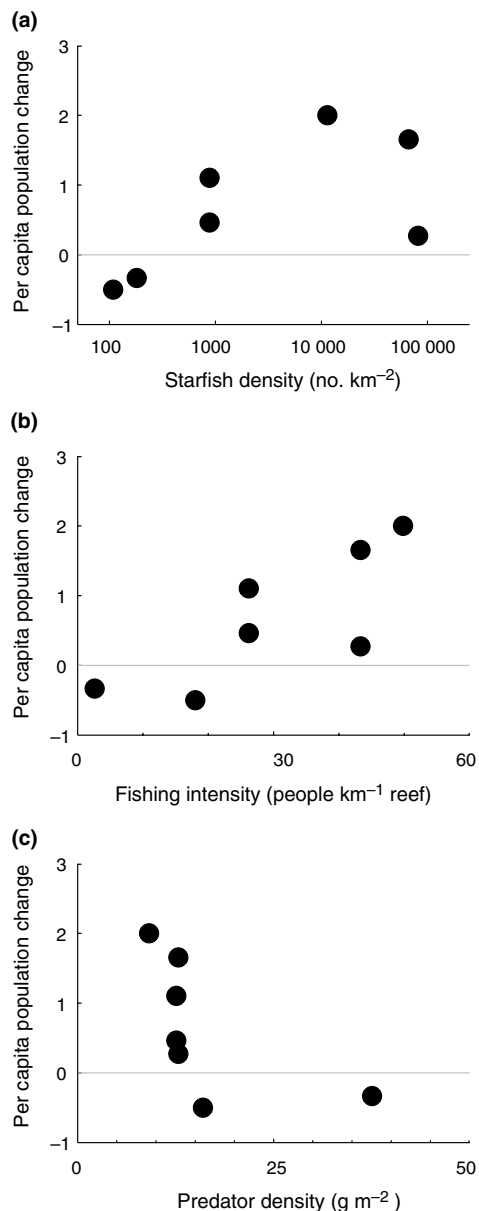


Figure 5 The relationship between per capita population growth of starfish and (a) average starfish density, (b) fishing intensity and (c) average density of predatory fishes. See methods for details of calculation of per capita population growth rate.

function. The higher densities of the coral-feeding starfish associated with subsistence fisheries exploitation have resulted in repeated shifts in benthic community structure from that dominated by carbonate accreting reef building organisms to domination by non-reef building organisms. This mechanism is consistent with other experimental and smaller-scale studies of terrestrial and aquatic systems which suggest consumer removal can have cascading effects upon ecosystem structure, function and diversity (Duffy 2003).

We have used a correlational approach to infer mechanistic links across trophic levels and in particular to infer that fishing intensity is the underlying causal factor. It should be borne in mind that causality can only be determined through experimental manipulation, thus we cannot exclude the possibility that the correlational link might be due to some other unknown factor associated with human population density and extent of coral reef. The relatively small spatial (1–100 km) and temporal (1 year) scale of our study limits the degree to which these findings can be extrapolated to other geographical areas and outbreak events. We attempted to include all possible starfish predators, but this broad-brush correlative approach using an aggregated carnivore guild runs the risk of attenuating or obscuring any single species predator-prey signal. This means our approach is conservative with respect to the hypotheses tested, at the expense of providing species-specific details of predator-prey interactions.

Our study focuses on the potential role of predators in controlling starfish dynamics and the evidence is elaborated upon in Appendix S2 (see Supplementary Material). However, this role must only be part of the explanation of starfish dynamics. Starfish were not observed at seven islands in this study, yet some islands overlapped in fishing intensity and predator density with islands where outbreaks occurred. We have only considered the link between starfish density and dynamics and an aggregated index of predator abundance, it is possible that a detailed examination of changes in species composition and functional attributes of the predator communities may help further explain variation in starfish density and dynamics. However previous work also suggests starfish outbreaks result from an interaction between predation and the variation in starfish recruitment – the recruitment-initiated predation hypothesis (Bradbury & Antonelli 1990; Ormond *et al.* 1990). Recruitment events of greater magnitude are required to swamp predators and outbreak in systems with higher predatory capacity. While bottom-up input of starfish recruitment is required to initiate events, the top-down predatory control modulates starfish recruitment into outbreaking or non-outbreaking populations. Both regional and local factors are thought to influence starfish recruit production and it may be worth quantifying recruitment and predation rates and processes to understand starfish dynamics and outbreak thresholds in Fiji and elsewhere in the Indo-Pacific region where outbreaks are known to occur.

The detection of phase shifts is fraught with difficulty, because of the nonlinear and dynamic nature of systems, and the problem of discerning causality at large spatial scales (Scheffer & Carpenter 2003). There are three features of these data which are consistent with thresholds and phase shifts (May 1977; Scheffer *et al.* 2001; Scheffer & Carpenter 2003). These features include the bimodal distribution of

starfish among islands, i.e. outbreaking vs. non-outbreaking populations (Fig. 2b), the observation that slightly differing initial states (predator densities/fishing intensities, Fig. 2a) lead to substantially differing final states (reef building vs. non-reef building taxa, Fig. 4) and the existence of thresholds and Allee-type dynamics (Fig. 5a–c). These results are entirely consistent with the existence of strong nonlinearity and threshold dynamics as a consequence of subsistence exploitation in one of the most pristine reef systems remaining today. While these islands may not be pristine in a historical context (*sensu* Jackson *et al.* 2001), they exhibit among the lowest known contemporary human population densities relative to coral reef area, on average Fiji has 83 people km⁻² reef area and these Lau Island study sites have human population densities ranging between two and 42 people km⁻² reef area (Table 1). By comparison, other major coral reef study sites are based in countries with comparatively high population densities, e.g. Australia, 391; St Lucia, 975; Hawaii, 1711; Jamaica, 2140; Philippines, 32 380; Kenya, 48 158 people km⁻² reef area (Appendix S1).

The rate of coral reef loss, at least in some parts of the world, is proceeding at a rate similar to or in excess of the rates of rainforest clear-felling (Gardner *et al.* 2003; Pandolfi *et al.* 2003). There is a good understanding of the mechanisms and importance of impacts such as hurricane disturbance, disease, coral bleaching and the effects of herbivore removal upon coral cover and reef health (Hughes *et al.* 2003; Hawkins & Roberts 2004). By comparison the impacts of predator removal on coral reefs have been relatively unstudied; this is not surprising given the large spatial scale of study required, the paucity of suitable study systems, the nonlinear dynamics and cross trophic level effects outlined above. These findings provide an additional challenge for biodiversity protection and coral reef management strategies. Starfish outbreaks have occurred on some Australian reefs nearly every decade in recent history despite the protection of the Great Barrier Reef Marine Park. These data suggest the maintenance of a minimum level of predators across reefs may be a useful management approach (Fig. 5c). Marine protected areas provide patches of elevated fish abundance in the face of exploitation (Roberts *et al.* 2001; Halpern & Warner 2002) and their utility in protecting reefs from pest outbreaks is worth exploring further.

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SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE593/ELE593sm.htm>

Appendix S1 Additional study details

Appendix S2 Can predators control starfish dynamics?

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